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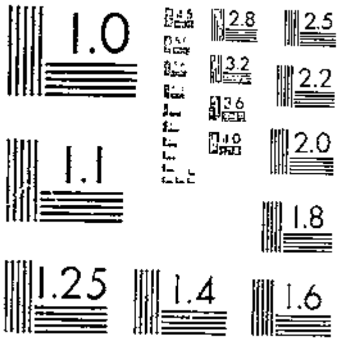

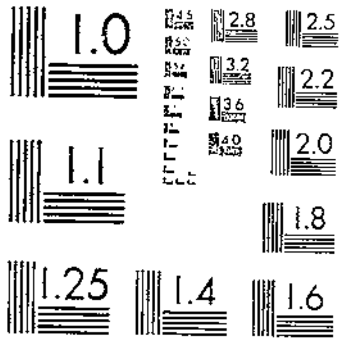

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STUDIES OF EXERISTES ROBORATOR (FAB.), A PARASITE OF THE EUROPEAN CORN BORER, IN THE LAKE ERIE AREA

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CONTENTS

INTRODUCTION

Exeristes roborator (Fab.) (fig. 1) is an ichneumonid parasite that develops externally on its host. It was found to be associated with the European corn borer (*Pyrausta nubilalis* Hbn.) in France early in the investigations initiated by the Bureau of Entomology to study the parasite complex of this insect pest in its native home, and subsequent extensive field observations (*3*, *4*)[2] have shown it to be fairly generally distributed throughout Europe. Thompson and Parker (*6*, *p. 34*) report, however, that "it is found most frequently in the southern part of the Continent."

The fact that it was among the first of the parasites found attacking the borer led to its importation and subsequent liberation in all the principal infested areas in the United States. In order to accomplish this distribution, extensive breeding was necessary, and during the course of this work an opportunity was presented to study the biology

[1] The observations recorded in this bulletin were made in connection with the parasite project of the European corn-borer investigations, D. W. Jones, in charge. The writers acknowledge the timely suggestions of D. J. Caffrey throughout the investigations and the preparation of the manuscript, Philip Luginbill's criticisms of the manuscript and preparation of photographic illustrations, H. L. Parker's comments on the status of the parasite in Europe, and the assistance of the various members of the staff in the accumulation of the laboratory and field data. Esther H. Hart made the drawing for fig. 1.

[2] Italic numbers in parenthesis refer to Literature Cited, p. 25.

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of the parasite under controlled laboratory conditions, its reaction to meteorological influences, and its seasonal synchronization with its host under controlled field-plat conditions, particularly in that part

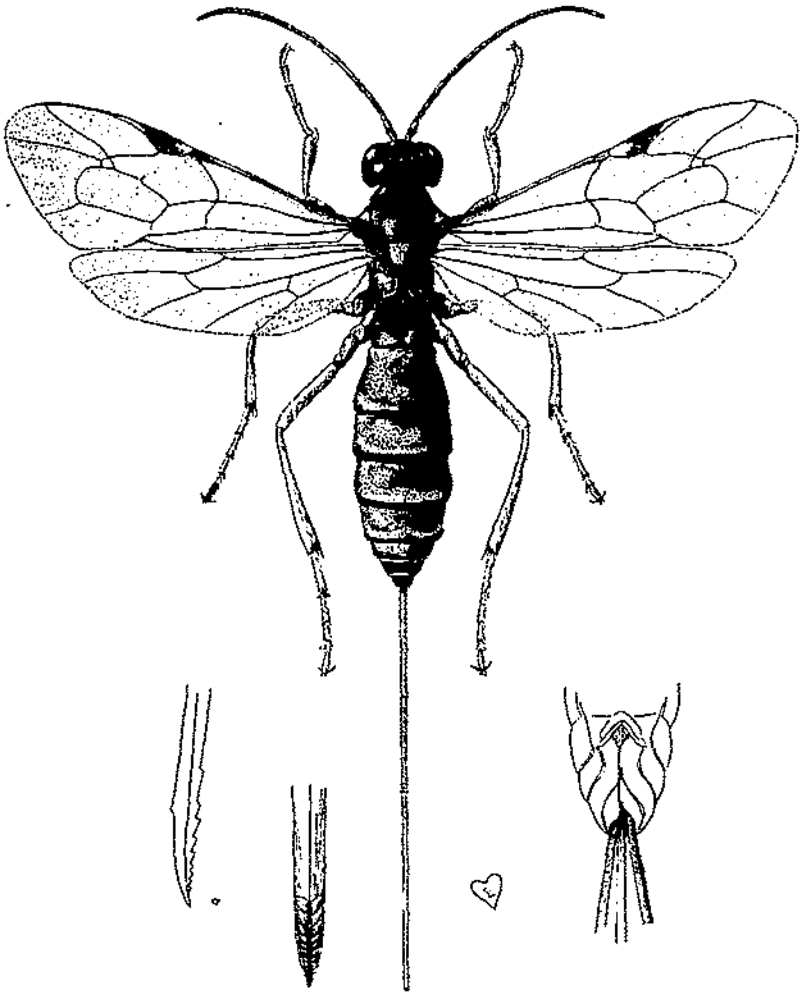


FIGURE 1.—*Exeristes roborator*, adult female and details.

of the one-generation area in the vicinity of Lake Erie. These studies were made principally at Monroe, Mich.

LABORATORY STUDIES

In developing a laboratory technic by which large numbers of adults might be produced, a study was made of the reactions of the parasite to the various artificial conditions imposed by a laboratory environment. Principal among these were reactions to temperature and moisture.

REACTIONS TO TEMPERATURE AND MOISTURE

Experiments to determine the effect of variations in temperature and moisture on the reactions of the parasite were divided into three groups: (1) The effect on the incubation of eggs; (2) the effect on the development between hatching of the eggs and emergence of the adults; and (3) the effect on reactions of adults.

INCUBATION OF EGGS

Three experiments were conducted to determine the percentage of hatch and the length of the incubation period when eggs were exposed to various temperatures and humidities.

In the first experiment a constant temperature of 80° F. and humidities ranging from 40 to 100 percent in 5 percent intervals were maintained. The results are presented in table 1. There is a noticeable increase in the percentage of hatch as the relative humidity increases from 40 to 60 percent, but beyond this point little difference is noted. There is also a slight acceleration of incubation as the relative humidity increases.

TABLE 1.—*Incubation of Exeristes roborator eggs at a constant temperature (80° F.) and varying relative humidity*

Relative humidity (percent)	Eggs	Hatch	Average incubation period	Relative humidity (percent)	Eggs	Hatch	Average incubation period
	Number	*Percent*	*Hours*		*Number*	*Percent*	*Hours*
40	100	60	30	75	50	90	27
45	50	68	29+	80	100	92	27½
50	100	80	28	85	100	91	27+
55	100	83	28	90	50	88	27
60	50	88	28	95	50	90	28
65	50	90	28½	100	50	85	28
70	100	92	28				

In a second experiment the relative humidity was constant at 70 percent and the temperature ranged from 45° to 110° F. in 5° intervals. The results are shown in table 2. A general increase in the percentage of hatch takes place throughout the temperature range from 45° to 80°, but at 85° a decrease in hatch begins and at 110° there is practically total mortality. A similar general effect is shown in the acceleration of incubation, although in inverse ratio. The length of the period is perceptibly shortened as the temperature is raised from 45° to 95°, but above 95° there is a slight increase.

TABLE 2.—*Incubation of Exeristes roborator eggs at a constant relative humidity (70 percent) and varying temperature*

Temperature (° F.)	Eggs	Hatch	Average incubation period	Temperature (° F.)	Eggs	Hatch	Average incubation period
	Number	*Percent*	*Hours*		*Number*	*Percent*	*Hours*
45	200	1	205	80	100	92	27
50	50	10	175	85	50	90	24
55	50	40	104	90	50	88	22½
60	50	58	58	95	100	80	21
65	50	70	48	100	50	68	22
70	100	94	36	105	50	40	23
75	50	92	30	110	50	2	24½

A comparison of tables 1 and 2 shows that temperature variations exert a far greater influence on incubation of *Exeristes roborator* eggs than do humidity variations.

Nevertheless, the necessity of changing moisture conditions to meet the requirements of different temperature influences apparently represented a critical phase in the rearing of the insect. The effect of different combinations of temperature and humidity within the range of practical working conditions is shown in table 3. It will be noted that at each temperature the percentage of hatch, and also, in lesser degree, the rate of incubation, tends to increase as the relative humidity is increased.

TABLE 3.—*Incubation of Exeristes roborator eggs at varying relative humidity and varying temperature*

Temperature (° F.)	Relative humidity	Eggs	Hatch	Average incubation period	Temperature (° F.)	Relative humidity	Eggs	Hatch	Average incubation period
	Percent	*Number*	*Percent*	*Hours*		*Percent*	*Number*	*Percent*	*Hours*
45	45	200	0	(1)		45	50	21	23½
	95	50	4	277		65	50	84	22½
75	55	50	80	33	95	70	100	81	22½
	70	50	92	30½		75	50	84	22½
	95	50	94	31		85	100	81	21

[1] No hatch.

In general, the incubation of eggs of *Exeristes roborator* is controlled rather definitely by temperature and relative humidity, the most favorable conditions being temperatures between 78° and 85° F. accompanied by relative humidities between 70 and 80 percent.

DEVELOPMENT FROM EGG TO ADULT

The percentage of larval survival and the length of the period from hatching to issuance of the adult were utilized as indices to the parasite's reaction to variations in temperature and moisture during this period. Following numerous preliminary observations that indicated an environment of 80° F. and 70 percent relative humidity to be suitable for this period of development, experiments were conducted to determine the effects of temperature and moisture variations on the percentage of larval survival and the rate of larval development. The results of these experiments are given in table 4.

TABLE 4.—*Survival and development of Exeristes roborator larvae when subjected to different temperature and moisture conditions* [1]

Temperature (° F.)	Survival at a relative humidity of—				Length of developmental period at a relative humidity of—			
	45 percent	70 percent	85 percent	100 percent	45 percent	70 percent	85 percent	100 percent
	Percent	*Percent*	*Percent*	*Percent*	*Days*	*Days*	*Days*	*Days*
63	20	46		34	35.0	30.7		34.0
70	20				28.2			
75		57	48	30		20.6	19.9	19.8
80	13	70	65	36	20.0	16.8	17.0	18.0
85	8	68	56	40	20.3	15.4	16.2	16.8
90	0				.0			
95	0	40			.0	18.7		
100		10	54	20		23.0	17.5	17.0
105		0				.0		

[1] 100 individuals utilized to obtain averages at each condition.

Survival was highest in an environment of 70 percent relative humidity and temperatures between 80° and 85° F., and the same environment also produced the shortest developmental period. Moisture, however, has a greater effect on the percentage of survival than it does on longevity, whereas the response to temperature variations is more rapid in rate of development than in percentage of individuals successfully completing their development. It is the opinion of the writers that, while the effect is more obscured than in the incubation period, higher temperatures should be accompanied by increased humidities, probably to counteract the increased tendency to evaporation. It will be noted that complete mortality occurred in the 45 percent humidity when the temperature was 90°, but that this did not obtain in the 70 percent humidity until the temperature was raised to 105°.

ADULT ACTIVITY

Although temperature and moisture changes definitely influence all phases of adult activity, such as movement, feeding, mating, and oviposition, only temperature changes result in pronounced variations in these activities. Moreover, it is only in extremes of temperature (below 50° and above 90° F.) that this factor tends seriously to restrict normal adult activities. The effects of varying temperatures and humidities on the length of adult life and on reproduction are, however, quite evident. The effect on longevity and reproduction of relative humidities of 45, 70, and 85 percent and temperatures ranging from 60° to 100° in 5° intervals is shown in table 5. As was evident in incubation and larval development, 80° and a relative humidity of 70 percent again approach very closely to the optimum conditions for adult activity.

TABLE 5.—*Length of adult life and oviposition of Exeristes roborator when subjected to different temperature and moisture conditions* [1]

Temperature (°F.)	Length of adult life at a relative humidity of—			Average number of eggs deposited by 1 female at a relative humidity of—					
				45 percent		70 percent		85 percent	
	45 percent	70 percent	85 percent	Daily	Total	Daily	Total	Daily	Total
	Days	*Days*	*Days*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
60	12	25	20	1	12	1	25	1	20
65	14	31	23	1	14	2	62	1	23
70	28	39	24	2	56	3	117	6	144
75	28	38	38	6	108	5	190	7	266
80	25	30	30	5	125	11	440	12	360
85	20	37	32	5	100	14	504	12	384
90	8	12	28	2	10	9	108	11	208
95	4	6	12	----	0	4	24	6	72
100	2	2	5	0	0	2	4	1	5

[1] 10 individuals utilized to obtain averages at each condition.

THE LARVAL DIAPAUSE

The requirement of *Exeristes roborator* for a resting period in its larval development has occasioned extensive observations in an effort to determine some of the causative factors. Seasonal influences have been studied, the type and quantity of food have been varied, and environments have been changed by manipulation of temperature and humidity. All these factors doubtless influence the tendency of the species to undergo a diapause. Observations on several generations of progeny of parents that had passed through the diapause, and of those that had not, failed to produce any evidence that heredity is involved. In all these investigations the results have been variable, and in many instances the variation between replications has exceeded variations between experiments too greatly to permit any definite conclusions to be drawn. This variability in the occurrence of the diapause among progeny of the same group of females that had received the same laboratory manipulation and developed under the same conditions is shown in table 6.

TABLE 6.—*Occurrence of the diapause in different progeny of a group of Exeristes roborator females that received the same laboratory manipulation and developed under the same conditions except for date of oviposition*

Date of oviposition	Individuals observed	Individuals in diapause [1]	Date of oviposition	Individuals observed	Individuals in diapause [1]
1931	*Number*	*Percent*	1931	*Number*	*Percent*
Jan. 19	17	58.8	Jan. 21	34	94.1
Jan. 20	59	58.1	Jan. 22	14	50.0

[1] Individuals were considered in diapause if no perceptible development could be observed during a 30-day period of exposure to a constant temperature of 80° F. and a constant relative humidity of 70 percent immediately following the formation of the cocoon.

It has been observed that almost any conditions adverse to normal development, such as restriction of food or changes of temperature and humidity from a favorable to an unfavorable condition, tend to cause some individuals to pass into a diapause. The recurrence of the diapause almost every year from November to March, as shown in table 7, is still unexplained. It seems to have no relation to the number of generations that have intervened since the last diapause, and in some instances individuals or groups of individuals develop to adults when 90 percent or more of others exposed to the same conditions will mature only after a resting period.

TABLE 7.—*The seasonal recurrence of the diapause in Exeristes roborator larvae* [1]

Year and month	Individuals observed	Individuals in diapause	Year and month	Individuals observed	Individuals in diapause
1928	*Number*	*Percent*	1930	*Number*	*Percent*
June	7,943	2	March	4,367	78
July	7,621	1	April	21,537	14
August	25,016	1	May	14,608	21
September	29,343	1	December	2,400	25
October	2,689	1			
November	1,000	40	1931		
December	1,000	40	January	12,000	20
			February	4,912	79
1929					
January	1,200	20			
February	10,740	23			
March	12,350	26			
April	25,600	58			

[1] All material was exposed to 80° F. and 70 percent relative humidity throughout the observations.

The conditions obtaining during this resting period exert a strong influence on both the rate of response and the eventual mortality of the individuals. A group of larvae in diapause were kept in an environment of 80° F. and 70 percent humidity until they either died or resumed development and became adults. Examinations at 10-day intervals, the first being made 10 days after the group had been determined in diapause, showed a very slow resumption of normal development and a mortality that increased gradually from 2 to 40 percent (table 8).

TABLE 8.—*Emergence and mortality of Exeristes roborator larvae in diapause, when reared at 80° F. and 70 percent relative humidity* [1]

Time after determined in diapause (days)	Emergence	Larvae remaining in diapause	Mortality	Time after determined in diapause (days)	Emergence	Larvae remaining in diapause	Mortality
	Percent	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*
10	2	96	2	60	8	82	10
20	4	92	4	70	12	76	12
30	4	88	8	80	14	74	12
40	6	86	8	90	22	60	18
50	6	84	10	100	60	0	40

[1] 100 individuals were utilized in this experiment.

Another group of larvae in diapause were placed in storage at 33°–35° F. and 70 percent relative humidity. Portions of this group were removed at 10-day intervals up to 90 days and subsequently at longer intervals, and then subjected to developmental conditions (80° and 70 percent humidity) for 30 days. The response of these individuals is shown in table 9. Complete elimination of the tendency to remain in a diapause is noted after 70 days' storage, and there was a gradual increase in emergence as the length of time in storage increased up to this point. The emergence occurred within 30 days of removal from storage, and all individuals that had not responded at the end of this period were considered as still in diapause.

TABLE 9.—*Emergence and mortality of Exeristes roborator larvae in diapause, when subjected to varying periods of storage at 33°–35° F. and 70 percent relative humidity, followed by 30-day exposures to 80° and 70 percent relative humidity* [1]

Time in storage (days)	Emergence	Larvae remaining in diapause	Mortality	Time in storage (days)	Emergence	Larvae remaining in diapause	Mortality
	Percent	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*
0	2	96	2	70	80	16	4
10	4	94	2	80	100	0	0
20	5	93	2	90	92	2	6
30	12	88	0	180	94	0	6
40	20	80	0	365	92	0	8
50	48	50	2	540	88	0	12
60	64	36	0				

[1] 100 individuals were utilized in each series.

Other attempts to break the diapause of this insect have met with little success. Subjecting the material in diapause to a higher temperature than that at which the condition was produced merely tended to increase the total mortality and the rate at which it occurred. Subjecting the individuals to severe shocks, such as holding them in a 17° F. environment for 24 hours and then immediately submerging them in water at 120° for 2 minutes, caused some resumption of development. Except where long exposures to low temperatures were provided, however, the mortality was too great to permit the successful application of any measure to break up the diapause period.

HABITS AND ACTIVITY

The life cycle of *Exeristes roborator* as determined in the laboratory cannot be used in interpreting the parasite's responses under natural conditions, because the influences involved in its development are not the same in both cases. The major factors affecting the life cycle have already been discussed, and the following presentation of the reactions of the parasite in the various stages of its cycle will supply the information essential to an understanding of the development of *E. roborator* in the laboratory.

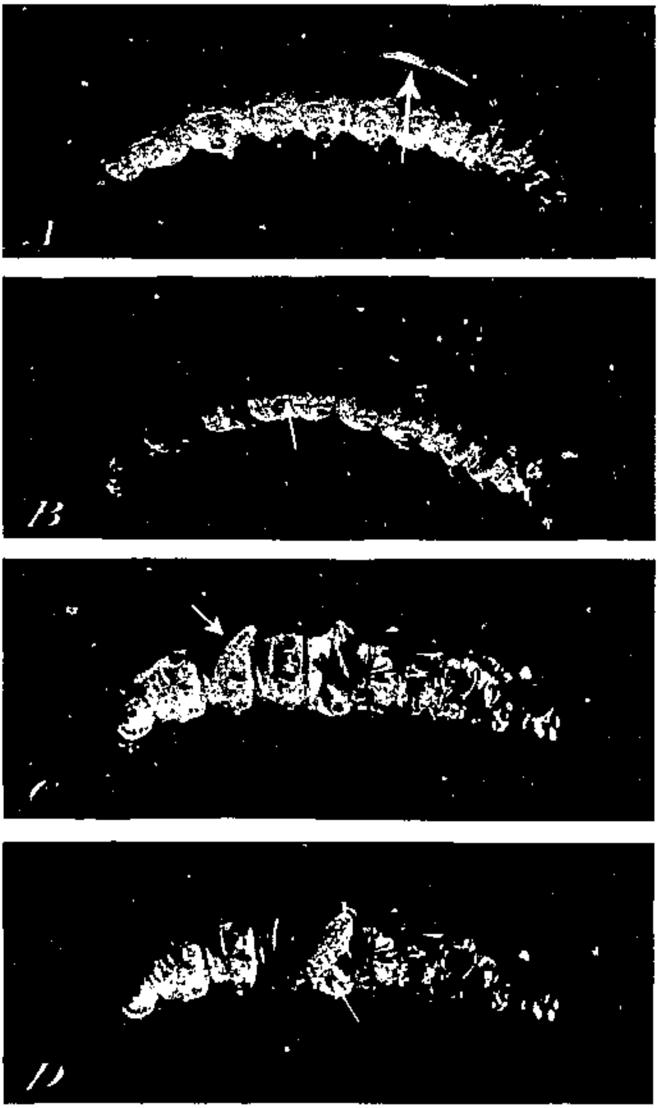
LARVA

The entire larval life of *Exeristes roborator* is spent in close proximity to its host, all feeding and development occurring externally. As soon as the young larva has cut its way through the chorion of the egg (pl. 1, *A*; pl. 2, *F*), it crawls about over the host, feeding at different places. To obtain food the larva presses its mouth against the borer, usually at some tender part of the cuticle such as the intersegmental skin, and with the mandibles cuts through the cuticle, holding the mouth firmly attached to the borer. The first-instar larva (pl. 1, *B*) feeds little, if at all, on solid food, depending for its nourishment on the blood of the host, which it extracts by a sucking process. The second-instar (pl. 1, *C*) larva feeds in the same manner, and not until the third-instar (pl. 1, *D*) is reached is feeding on the fat content of the host noted. The fourth-instar larva (pl. 2, *A*) consumes more of the body content of the host and eats freely of the fatty tissue. The fifth-instar larva (pl. 2, *B*) finishes consumption of the host, leaving only its head, outer cuticle, and other more solid portions.

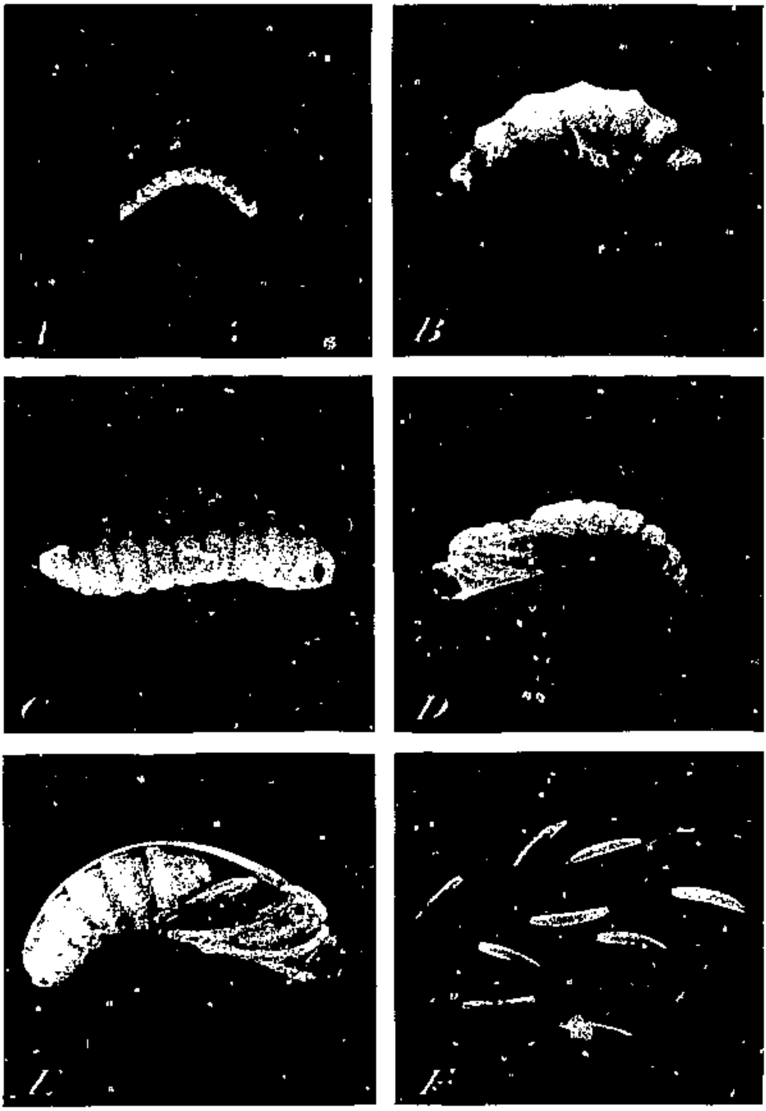
When it is fully fed, the larva rests for 20 to 36 hours. It then spins a cocoon of loosely woven silk, which finally assumes a parchmentlike texture following the exudation of a viscous fluid which the larva deposits on the silk strands. After the larva has spent from 36 to 72 hours in the cocoon, the prepupal stage (pl. 2, *C*) becomes evident. Before the pupal molt takes place, however, some of the semiliquid meconium is deposited as 15 to 50 small pellets.

PUPA

Following the prepupal stage from 5 to 7 days is spent in the pupal stage (pl. 2, *D* and *E*). During this stage there is usually



Immature stages of *Exeristes roborator* on *Pyrausta nubilalis* larvae in situ: *A*, Egg; *B*, first-instar larva; *C*, second-instar larva; *D*, third-instar larva. × 3½.



Immature stages of *Exeristes roborator*: *A*, Fourth-instar larva; *B*, fifth-instar larva; *C*, prepupa; *D*, male pupa; *E*, female pupa; *F*, eggs. ×3½.

considerable movement within the cocoon. The insects go through many contortions, revolving, bending, and pivoting on each end for hours at a time.

ADULT

When ready to emerge, the adult cuts a ragged hole in the cocoon, much larger than is necessary, and crawls through. Usually the first act after emergence is to void from one to several drops of yellow meconium. It then cleans its appendages by stroking one over the other and straightens out any portion that may be crooked. The grooming complete, the adult seeks food and water, of which it takes small quantities at irregular intervals during the first few days.

The time of mating depends on the sex. The males make no attempt to mate during the first 12 hours after emergence, and only rarely until after 24 hours. They usually become aggressive in from 36 to 48 hours and continue so until shortly before death. The longevity of a male is inversely proportional to the frequency of mating.

In the case of the female, however, mating may occur immediately upon emergence or at any time during the first 72 hours of adult life. Females usually mate several times when associated with males during this period, but when 72 to 96 hours have passed, or oviposition has begun, mating is restricted to females that have not previously mated, and such females mate only once. Although mating of *Exeristes roboratar* is dependent upon the age of the male, there is little difficulty in obtaining satisfactory mating under laboratory conditions. The male emerges 1 or 2 days earlier than the female and becomes sexually mature in 12 to 48 hours, thus synchronizing with the delayed emergence of the female.

The female always oviposits on borers that are concealed as they are usually found in cornstalks. She locates the host in the stalk apparently through a sense of smell, as often the spot at which she thrusts her ovipositor is merely a location where the borer has been. The act of oviposition in this species requires from 3 to 5 minutes, since the female invariably paralyzes the host before depositing an egg on it. When encountering a borer, she thrusts her ovipositor into its body, moves it forward and backward, up and down, and to each side again and again until the borer ceases to move or until the instinct to kill the host has been satisfied. The resulting paralysis may be either mechanical or a stupor produced by a poison exuded from the sting, probably both. A single thrust of the ovipositor is sufficient to stupefy the borer for 2 or 3 days and may even cause its death. The mechanical effect of inserting the ovipositor or a similar object is also enough to kill the borer, as has been determined through mechanical paralyzation. As soon as the borer is paralyzed or killed, the female deposits an egg on or near it.

Under laboratory conditions the female *Exeristes roborator* seems to have little preference either for a specific host or for a particular instar when ovipositing on *Pyrausta nubilalis.* Oviposition has occurred on all the instars of the host from the second through the full-fed larva, but no parasites were produced when oviposition was upon any instar previous to the fifth. A female may oviposit many times on a borer, and several females may oviposit on the same borer.

The parasite seems to have no means of distinguishing parasitized from unparasitized borers; in fact, parasitized borers were more attractive in test material.

There is considerable variation in the time of day at which oviposition begins and in the number of eggs deposited by different females. It is thought that under natural conditions oviposition occurs only during the day. Light stimulates the female to activity, provided the temperature and other conditions are favorable. There is no apparent variation in the response of *Exeristes roborator* to different kinds of light. There are, however, differences that occur over short periods which may affect the normal oviposition; e.g., there is no oviposition for 36 to 48 hours after females are moved from a lighted into a totally dark environment. Either continuous light following 24 hours' darkness or intermittent light (12 hours dark and 12 light) abnormally increases oviposition over a period of 48 to 72 hours. Normal deposition, however, is resumed in either total darkness or continuous light if the adults are retained in either for 4 or more days.

Therefore, artificial light stimulates the female to activity just as natural light does and, other factors being equal, oviposition occurs at a similar rate. After oviposition has started, it proceeds normally subject to the influence of temperature variations, the numbers of eggs deposited increasing as the temperature is raised until the maximum production is attained and then decreasing rapidly.

The number of eggs deposited by different females in 1 day and during their entire life varies enormously. The reason for this variation is not known. However, since females that are induced to oviposit where no borers are available for food deposit very few eggs, it may be assumed that oviposition is dependent to a certain extent upon the presence of some food other than sugar. On the other hand, some females are more productive than others. This may be due to differences in size, in available food, in natural potential, etc., and is not peculiar to *Exeristes roborator*. Thus, in the summer of 1929 isolated females kept under field conditions deposited from 1 to 9 eggs per day and the total deposition per female ranged from 1 to 83. A similar group of isolated females maintained in the laboratory deposited a minimum of 1 egg and a maximum of 40 eggs per day, or an average of from 1 to 13 per female, and the total deposition per female ranged from 115 to 679.

REARING METHODS

After the practicability of rearing the parasite in the laboratory had been ascertained, a breeding technic was evolved by Thompson (*5*). It was immediately appreciated that the development and refinement of this technic would provide a source of adults for liberation purposes that would be much more economical and practical of operation than continued importation of field-collected material (*2, pp. 8–14*). This technic has been improved by the writers and has been utilized to supply practically all adults of this species released in the United States and Canada. The various steps in the technic as it has been utilized at the Monroe, Mich., laboratory are presented to indicate the possibilities of using such a procedure with other insects of the same type as *Exeristes roborator*.

COLLECTING ADULTS

Immature forms of *Exeristes roborator*, obtained from developing stock or from storage, are placed in an emergence cage (fig. 2, *A*). As the adults emerge, they are transferred to a compartment cage for

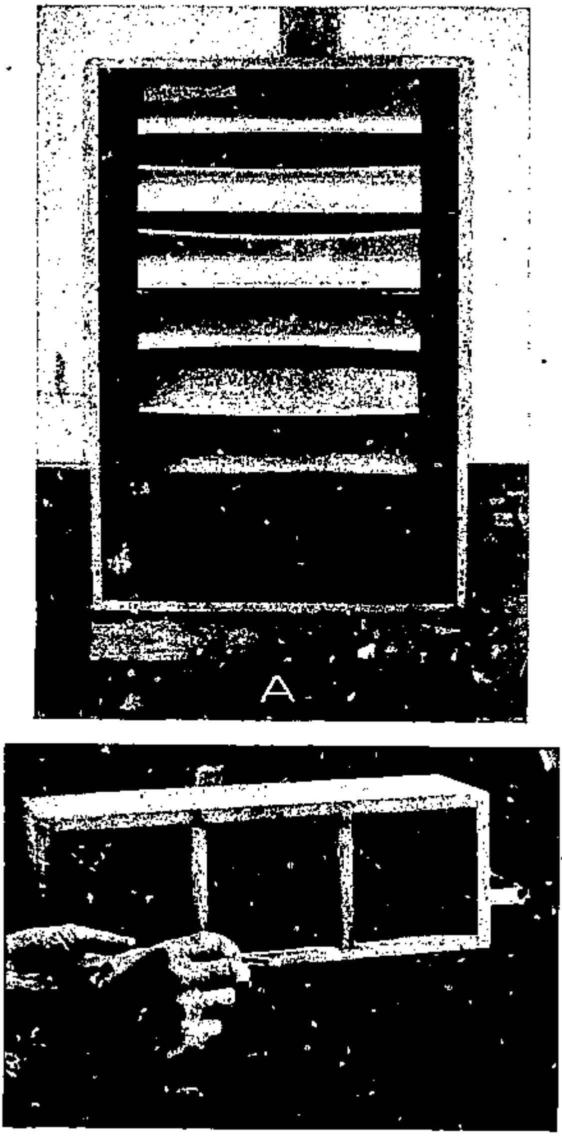


FIGURE 2.—*A*, Emergence cage; *B*, oviposition cage, for *Exeristes roborator.*

oviposition (fig. 2, *B*). Each compartment contains loaf sugar and cotton saturated with water in addition to a corn pith containing paralyzed *Pyrausta nubilalis* larvae. During the first 5 to 7 days 6 males and 6 females are maintained in each compartment, the males to insure fertilization of any females that did not mate in the emergence cage. The males are then removed, as they tend to interfere with normal female activity when confined in cages. The females that die are replaced by living females, and empty compartments are refilled with new males and females. All compartments are maintained in a sanitary condition at all times. The cotton is moistened and both cotton and sugar are replaced when necessary.

ARTIFICIAL PARALYZATION

As natural paralyzation of borers by *Exeristes roborator* is impracticable for quantity production of the parasite in the laboratory, various methods of accomplishing this artificially were tested. The method finally adopted consists of immersion of the borers for 10 minutes in water having a temperature of exactly 49° C. (120.2° F.). Higher temperatures or longer immersion tends to harden the borers so that they are unsuitable for feeding purposes, and lower temperatures or shorter exposures will not paralyze them. Clean, fresh water is used each day, and the container (fig. 3, *A*) utilized to hold the borers must also be clean. The water in which the container is immersed must be of sufficient volume to maintain a constant temperature when the borers are placed in it. The borers are scattered thinly over a tray and allowed to dry (fig. 3, *B*). Borers having an excess of moisture on them are not used, as they are liable to develop rot or become moldy.

OVIPOSITION PITHS

In order to facilitate oviposition and the manipulation of the eggs, oviposition piths are prepared by hollowing out sections of cornstalks on one side, and covering the groove with paper (fig. 4, *A*) held in place with rubber bands. One of these piths containing paralyzed borers in the groove is placed in each compartment of the oviposition cage (fig. 2, *C*). Care must be used to place the pith firmly against the glass front of the compartment with the grooved surface up. Since many eggs hatch in less than 48 hours in the incubation environment, the piths are replaced daily. This operation is performed with the glass front of the cage facing the light.

CARE OF EGGS

In order to obtain the maximum number of parasites from available eggs, each egg must be isolated on a separate host. Accordingly, one paralyzed borer is placed at the bottom of each of as many vials as necessary (fig. 5, *A*). For ease of handling, the vials are placed in racks (fig. 4, *B*) and a number of these racks are carried on a tray (fig. 4, *C*). After the borers have been placed in the vials, the parasite eggs are transferred from the piths to a smooth, sterilized surface. One egg is then placed on each host with a small camel's-hair brush (fig. 5, *B*). The brush should be kept moistened with distilled water while in use. All the material is then placed in the incubator room at 80° F. and 70 percent relative humidity for hatching and larval development.

CARE OF LARVAE

The developing material requires no attention for 5 days, at the end of which time the first cocoons appear, indicating conclusion of

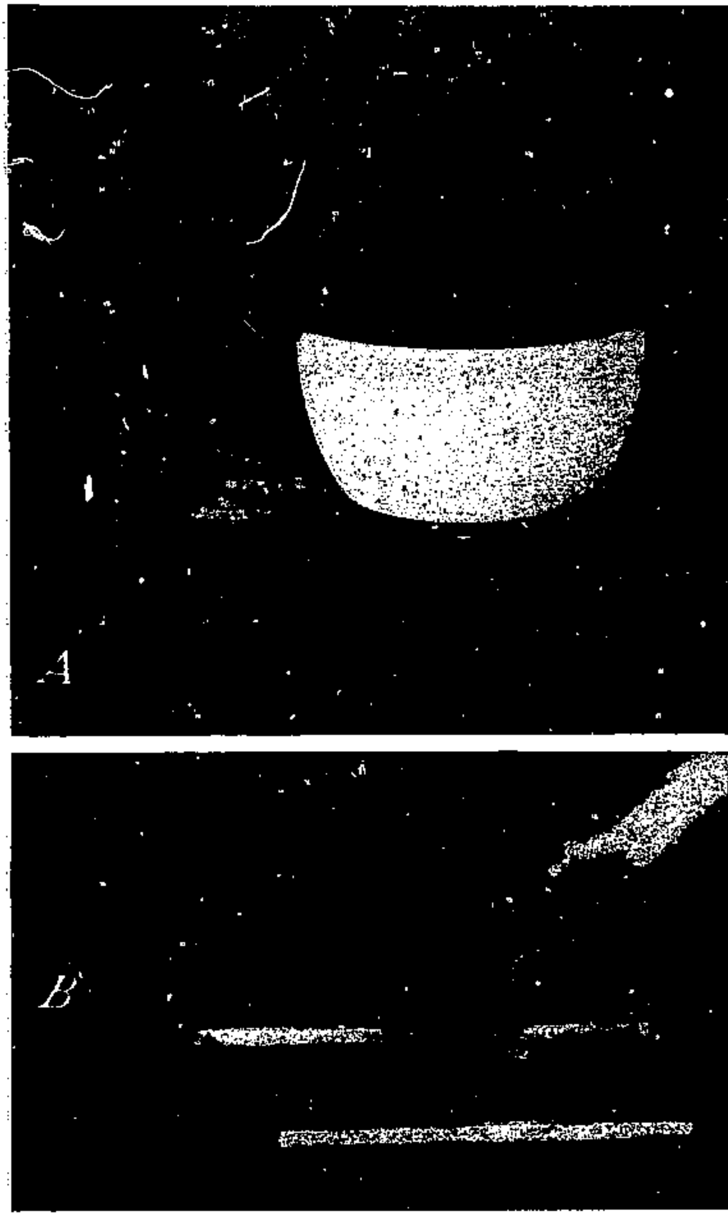


FIGURE 3.—*A*, Container for immersion of *Pyrausta nubilalis* larvae in water; *B*, drying paralyzed *P. nubilalis* larvae.

the larval period. Examinations are then made every second day and vials containing cocoons or dead parasite larvae are removed from the racks, and the borers in the remaining vials that are no longer suitable food are replaced.

CARE OF COCOONS

The handling of the cocoons is contingent on the purpose for which they will be used. If additional breeding stock is required or if a liberation program is in progress, they are placed in an emergence cage for adult emergence and disposition. If, on the other hand, and as is the more usual circumstance, the cocoons are produced in the course of breeding looking toward liberations several

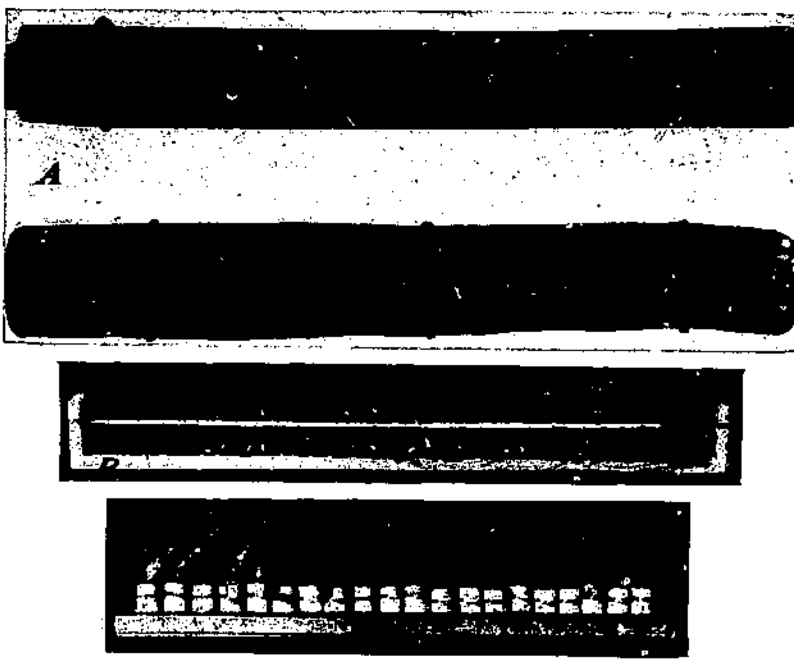


FIGURE 4.—*A*, Oviposition piths in cornstalks; *B*, rack with vials; *C*, tray with racks and vials, for rearing *Excristes roborator*.

months in the future, they must be treated with special care to avoid disastrous mortalities.

STORAGE

The problem of proper storage arises because of the necessity of synchronizing liberations of the parasite with the presence in the field of the host in a suitable condition for parasitization. The fact that there is only a short period in which synchronized liberations can be made precludes the accumulation of a sufficient quantity of adults for liberation purposes except over a much longer period of laboratory production. This restriction necessitates the emergence of adults, when liberation is being accomplished by release of adults, over a much shorter period than is required to bring the desired number of individuals up to emergence. A method had to be devised, therefore, to induce varying degrees of delayed emergence of the parasite.

This has been accomplished by placing either the pupa or the larva when in the diapause in cold storage at 32°–40° F. and a relative humidity of 75 to 90 percent. Temperatures higher than these were found to permit an undesirable development, while lower temperatures caused malformed individuals to emerge and in some cases increased the mortality of all material. *Exeristes roborator* pupae and larvae in diapause can be retained in storage under these conditions for 6 months with no evident harmful effect on subsequent development, and larvae in diapause can be kept as long as 10 months with a negligible increase in mortality.

It is important that the material be prepared properly for cold storage. Insulation with 4 to 6 layers of heavy wrapping paper should be provided to prevent evaporation of moisture and to regulate the temperature (fig. 6, *A*). Exposure of the material to the storage environment and the return to developmental conditions should be gradual, with not more than a 10° change in temperature in 1 day.

FIGURE 5.—*A*, Filling rearing vials with European corn borers paralyzed by immersion in hot water; *B*, transferring *Exeristes roborator* eggs onto paralyzed hosts.

EMERGENCE

After the material has been removed from storage, it is treated in the same way that nonstored pupae and larvae are treated; that is, it is placed in an emergence cage in the incubator room, and the emerging adults pass from this cage into the migration cage (figs. 6, *B*, and 7, *A*). The adults are then removed from the migration cage and prepared for liberation in the field. This preparation consists of dividing the adults into colonies, balancing the sex ratio, feeding, watering, and retention in an environment conducive to mating for at least 24 hours prior to release in the field.

FIELD STUDIES

Following several seasons' unsuccessful attempts at colonization of *Exeristes roborator*, field investigations were started in an attempt to find out why this parasite is unable to maintain itself in the Lake Erie area. Field plats and cages (fig. 7, *B*) were utilized in order to render material available for observation. Although these artificial conditions did not duplicate the natural environment of the parasite, they were sufficiently close to permit the observations to be applied in interpreting the field status of the parasite in the environments studied.

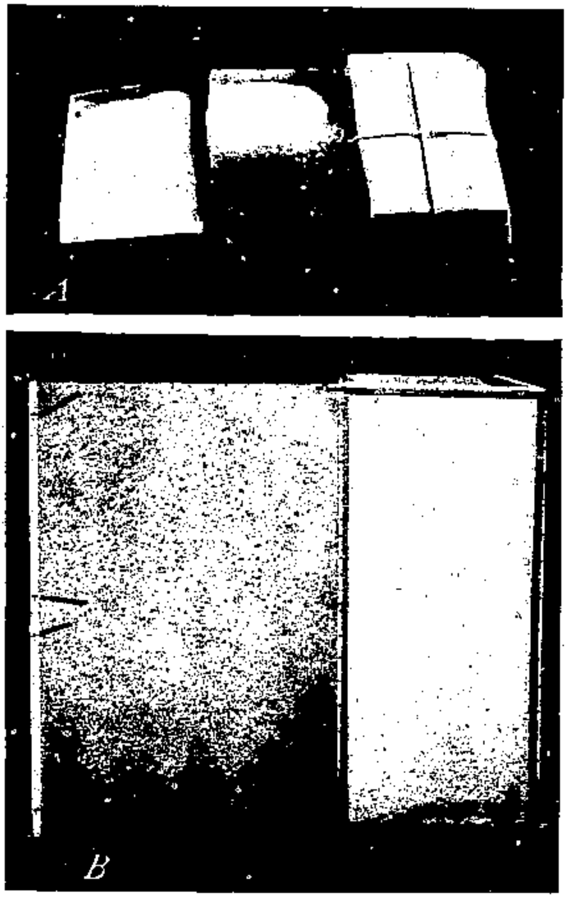


FIGURE 6.—*A*, Preparation of *Exeristes roborator* larvae and pupae for storage; *B*, emergence cage, with migration cage attached, for *E. roborator*.

CLIMATIC INFLUENCES

One of the first considerations was the direct effect of meterological conditions prevailing in this area. From field observations following liberation and initial establishment on full-fed host larvae in the fall, it was early determined that the parasite was capable of withstanding winters in this area. It was also observed, however, that continued maintenance failed and that the only parasites that survived the winter were those reared from adults released late in the summer or in the fall. Accordingly, observations were continued for an entire season, during which a supply of host larvae suitable for parasitization was kept available at all times when the parasites might be active. With these precautions no difficulty was encountered in rearing successive generations of the parasite from one year to another.

It is appreciated that the efficiency of the parasite might be affected by certain climatic conditions that do not as yet appear.

LIFE CYCLE

In order to determine the relationship between *Exeristes roborator* and *Pyrausta nubilalis* and the requirements for successful parasitization, a study was made of the life cycle of the parasite.

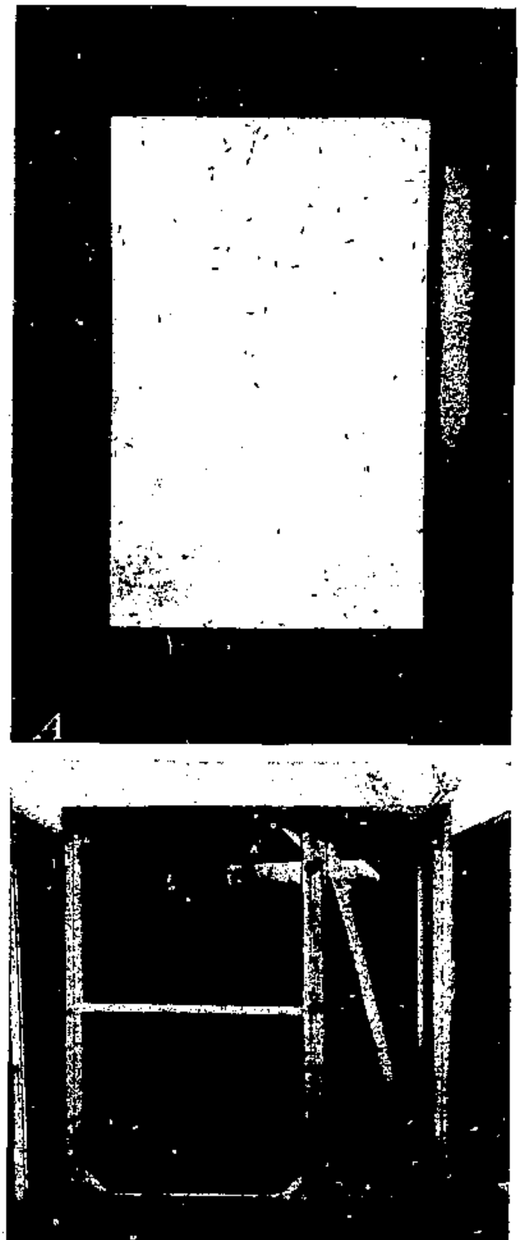


FIGURE 7.—*A*, Migration cage for *Exeristes roborator*; *B* field cage on weeds and debris during hibernation.

RELATIONSHIP BETWEEN DEVELOPMENT OF HOST AND PARASITE

The first study was to determine the limits of host development that would support the parasite to maturity. The results of exposure to the parasite of *Pyrausta nubilalis* larvae in different stages of development are given in table 10.

TABLE 10.—*Development of Exeristes roborator following the parasitization of various stages of Pyrausta nubilalis larvae*

Stage of *P. nubilalis*	Specimens used	Effect on host other than paralysis	Host condition following parasitization	Degree of parasite development
	Number			
Third	200	Bled	Dried	First and second instars.
Fourth	200	do	do	Second and third instars.
Early fifth	200	None	Rot and food shortage	Third and fifth instars.
Full-fed	50	do	Rot	5 percent emergence.
Late full-fed	50	do	Sound	20 percent emergence.
Hibernating	50	do	do	60 percent emergence.

It is evident that development of succeeding generations of parasites is dependent upon the availability of host larvae that have reached their fifth instar when the oviposition period of the parasite occurs. The parasite will, however, attack and kill borers in other stages of larval development, and thus cause an immediate reduction in their number. The data suggest two possible explanations of the nonsuitability of borers in the early instars to serve as hosts for the parasite. The first is that the physiological condition of the host brought about by the sting of the parasite—that is, excess bleeding or other breaking down of vital functions—may bring disaster to the developing parasite larva. The second is primarily the limited quantity of food available in the early instars of the host. The immediate effect is the production of smaller parasites, and finally the parasite larva becomes so weakened that it cannot perform its normal functions of pupation and emergence.

AVERAGE CYCLE IN THE LAKE ERIE ENVIRONMENT

Life cycles of many *Exeristes roborator* have been carried through on hibernating *Pyrausta nubilalis* larvae. Although wide variations will occur as conditions (particularly temperature) change, a cycle that may be expected under normal conditions during the active period in the Lake Erie environment is briefly outlined in the ensuing discussion.

In emerging, the adult cuts a ragged hole through the cocoon and escapes into the borer tunnel. It then cuts a round, smooth hole in the stalk and through it escapes to the open air to search for food. Both males and females have been observed feeding freely on sweet material such as honeydew and nectar. The females also feed extensively on paralyzed borers prior to oviposition, and during the oviposition period this is almost their only source of food.

Mating may occur immediately upon emergence of the female and continues throughout the preoviposition period, as was found to be the case in the laboratory. After a preoviposition period of from 5 to 7 days, the female locates prospective host larvae, paralyzes them, and then deposits one or more eggs on or near each larva. It has been observed many times that the female will deposit her egg regardless of the condition or suitability of the host, choosing a partially eaten larva just as readily as one in perfect condition to develop the parasite. Furthermore, several females may deposit eggs on the same host larva. Although multiple parasitism occurring from the activity of a single female is rare, as many as three eggs have been noted that have been deposited on a single host larva under conditions fairly comparable to those that obtain in nature.

Oviposition continues for 18 to 20 days. After the egg hatches, which is from 36 to 48 hours after its deposition, the young larva immediately starts feeding externally on the host, as described under the laboratory studies. Feeding and development continue for 7 to 9 days, and then the parasite larva is full fed and spins its cocoon in the borer tunnel. It remains as a larva within the cocoon for 5 days, pupates, and emerges 10 days later, thus completing a cycle from adult to adult in about 29 to 33 days.

As determined in extensive laboratory examinations, females of *Exeristes roborator* have an average potential reproductive capacity of about 350 eggs, which can readily be realized under laboratory conditions. This potential, however, is greatly reduced in the field. It dropped to 50 under cage conditions, which are considered more favorable than natural field conditions. All observations in this area have indicated that under field conditions the parasite has difficulty in locating hosts, and this is probably the chief factor contributing to the low reproductive ability of the parasite when released in natural environments.

SEASONAL HISTORY

One of the most important factors controlling the efficiency of a parasite is the synchronization of its life cycle with that of its host. Accordingly, the seasonal history of *Exeristes roborator* has been observed both in the laboratory and in field cages.

WITH HOST MANIPULATION

The first seasonal-history studies were conducted without regard to normal host development, the natural supply of hosts being supplemented at any time when numbers in the experiments became limited or when they were not normally present in the field. Under these conditions the parasite completed either 3 or 4 generations in this area, the number being dependent on individual differences rather than on climatic restrictions. The natural variation in the rate of development of different progeny of the same parents permits the earlier maturing forms to complete 4 generations while more slowly developing forms can complete but 3 generations during the period available for insect activity in the Lake Erie area.

The parasites begin emerging from hibernation between May 5 and 17, and emergence continues for from 20 to 30 days. From May 15 to September 15 a generation is completed every 30 days, but there are no well-defined points marking the end of one generation and the beginning of the next. Accordingly, except for a brief period in the spring immediately following resumption of activity, all stages of the parasite may be encountered at any time of the season. A certain percentage of the larvae in each generation enter a diapause, the smallest percentage in the spring with an increase to an average of 50 percent as winter approaches.

Most of the larvae that do not enter a diapause die during the cold weather. Pupae withstand the rigors of winter fairly well, and they resume active development immediately when the temperature becomes favorable, and often adults emerge so late in the fall or early in the spring that there is no opportunity for oviposition. It has been concluded, therefore, that the full-fed larva that has been in diapause is the true hibernating stage of *Exeristes roborator*, all other stages occurring during the winter being more or less incidental and subject to complete mortality in accordance with climatic conditions.

WITH NATURAL DEVELOPMENT OF HOST AND PARASITE

Attention was next centered on the seasonal cycle of *Pyrausta nubilalis* that prevails in the area under discussion. These observations were conducted in field plats, cages being used to prevent adult dissemination. One plat contained an abundance of overwintering *P. nubilalis* larvae naturally established in cornstalks and other debris. A second plat was planted to corn and the plants were artificially infested with *P. nubilalis* larvae concurrently with natural field deposition. At the time of the first natural emergence of adult parasites, *Exeristes roborator* adults were released in a cage placed over the hibernating host material. Mated female parasites were added to the original stock throughout the spring-emergence period of the parasite in order to maintain the original number released in the cage. *E. roborator* can complete but a single generation on hibernating *P. nubilalis* larvae in the Lake Erie area, as the supply of host larvae is exhausted by pupation when the first-generation parasite adults begin to emerge. Therefore, as soon as the adults of the first generation of parasites emerged, they were transferred from the hibernation cage in the first plat to the cage in the second plat containing developing *P. nubilalis* larvae. The parasites were supplemented occasionally by adults from other sources to insure the presence of an ample supply of ovipositing females.

Throughout the period of these releases first- to fourth-instar hosts were present, but no parasite larvae developed beyond the second instar. The last-emerging individuals of the first generation invariably were ready for oviposition prior to the appearance in the field of host larvae in a condition suitable to be parasitized and to support the developing parasite to maturity. The only exception was found in parasite larvae that underwent a diapause in the first generation. Adults from these individuals, however, do not emerge until the following spring, and the numbers are so small that they are of negligible importance.

A study of the seasonal histories of *Pyrausta nubilalis* (*1*) and *Exeristes roborator* indicates that one of the chief obstacles to the maintenance of *E. roborator* is that during the period of parasite activity, from May 15 to September 24, its host is present in the field in a stage of development capable of supporting *E. roborator* for only 2 months, from May 15 to June 15 and from August 24 to September 24.

WITH PARASITE MANIPULATION

A third series of tests was conducted in which the parasite was manipulated to suit the seasonal cycle of the host. In these tests stock material of mated *Exeristes roborator* females was introduced, at 2-week intervals throughout the developmental period, into field-plat cages containing normally developing host larvae. Periodic dissections of the host-plant material revealed that in no case was *E. roborator* able to become established until full-fed host larvae became available.

These observations give further proof of the poor synchronization of the seasonal cycle of *E. roborator* with that of *Pyrausta nubilalis*, and indicate that under these conditions *E. roborator* cannot be expected to become an important factor in the biological control of the European corn borer.

ALTERNATE HOSTS

Attention was then directed to the possibility of alternate hosts supplying the requirements of *Exeristes roborator* that are so evidently missing in *Pyrausta nubilalis*. Thompson and Parker report that in Europe *E. roborator* (*6, p. 34*)—

is apparently very polyphagous, attacking the larvae of both Lepidoptera and Coleoptera. The species on which it preys seem, however, all to be like *Pyrausta*, insects such as the clearwing moths (*Sesia* spp.), and the weevil *Cryptorrhynchus lapathi* L., which in the larval stage are borers living in tunnels in various plants.

Accordingly, a number of hosts that are present in appreciable numbers in the Lake Erie area were tested in both laboratory and field-plat experiments. Many of them were found to be unable to support the parasite because of their physical or physiological characteristics. Such proved to be the case with the *Papaipema* group, the parsnip webworm (*Depressaria heracliana* DeG.), and the cattail borer (*Arzama obliqua* Walk.). Other species were well adapted to parasitization by *Exeristes roborator*. These species included the elder borer (*Achatodes zeae* Harr.), the codling moth (*Carpocapsa pomonella* L.), and two species of *Pyrausta* (*ainsliei* Hein. and *penitalis* Grote). With the exception of *P. ainsliei*, however, the seasonal cycle diverged farther from that of *E. roborator* than does *P. nubilalis*, making them incapable of assisting in maintaining the parasite, although they served as an additional potential host supply when available.

Because in this environment the seasonal cycle of *Pyrausta ainsliei* agreed with that of *E. roborator* better than did that of any other species observed (not excepting *P. nubilalis*), more extensive tests were made to determine its actual suitability as a host for *E. roborator*. Although synchronization with *P. ainsliei* is closer than with *P. nubilalis*, similar limitations prevent maintenance of this parasite throughout its active period when this species (*P. ainsliei*) is the only host present. It is possible that this critical period in the parasite's development may be bridged by utilizing both *P. nubilalis* and *P. ainsliei* as hosts in areas where they are both present in sufficient numbers. It has been observed that the latest emerging individuals of *E. roborator*, produced in the spring on *P. ainsliei* borers that have overwintered, could be present in the field when the earlier developing *P. nubilalis* larvae have progressed sufficiently to enable them to support the progeny of these late-emerging parasites. For this phenomenon to be successful, an extremely delicate adjustment of seasonal cycles of *E. roborator* and these two hosts must be maintained, and therefore the ultimate result would not tend to increase the abundance of the parasite materially.

FIELD STATUS

In the environments under observation there was no evidence that *Exeristes roborator* is capable of maintaining itself in the Lake Erie area at present (1933) infested with *Pyrausta nubilalis*. A number of colony releases resulted in its initial establishment, but without producing succeeding generations.

This apparent inability of the species to persist from one season to another is shown by the liberation and recovery data assembled in table 11. The data summarize observations over a period of 7 years in all localities where adequate attempts at recovery were made. The 1927 and 1928 seasons have been divided into three periods—the first extending from May 5 to June 15, when suitable hibernating larvae of *Pyrausta nubilalis* are available in the field; the second, from June 15 to August 10, when host larvae, although present in the field, are unsuited to support the parasite to maturity; and the third continuing from this date, at which time host larvae are still unsuited to support the parasite but are sufficiently developed to reach the fifth instar before the end of the oviposition period of parasites emerging on August 10 or thereafter. In the last four seasons all releases were made prior to June 15. The recoveries and collections were recorded the spring after the date recorded in the table. In each locality where recovery was made, the entire supply of cornstalks from the field (10 to 14 acres) was placed in a cage the spring following the release before they could be exposed to any parasite activity other than that occurring during the season indicated. It is estimated that at least 250,000 *P. nubilalis* larvae were contained in the stalks placed in each cage. In all other instances recovery attempts were made by collecting samples of 500 corn borers at random from fields in the immediate vicinity of the liberation point.

TABLE 11.—*Releases of Exeristes roborator at all points in the Lake Erie area at which adequate attempts at recovery were made*

Locality	Number of *Exeristes roborator* adults released at the time indicated									
	1927			1928			1929 [1]	1930 [1]	1931 [1]	1932 [1]
	May 5 to June 15	June 16 to Aug. 10	After Aug. 10	Before June 15	June 16 to Aug. 10	After Aug. 10				
Monroe County, Mich	6,175	2,495	[2] 5,674 (R)	1,866	1,662	8,215 (R)	[3] (C)	(C)	(C)	(C)
St. Clair County, Mich	2,781		1,116 (R)	2,451	1,948	1,700 (R)	(C)	(C)	(C)	(C)
Lucas County, Ohio	3,482		(C)	2,000	2,095	3,622 (C)	(C)	(C)	(C)	(C)
Erie County, Ohio	2,000		(C)			(C)	(C)	(C)	(C)	(C)
Steuben County, Ind							3,997 (C)	1,993 (C)	(C)	(C)
Summit County, Ohio							3,975 (C)	1,985 (C)	(C)	
Cattaraugus County, N.Y							3,998 (C)	1,989 (C)	(C)	(C)
Wyoming County, N.Y							2,700 (C)	1,974 (C)	(C)	(C)
Oakland County, Mich							3,985 (C)	1,996 (C)	(C)	(C)
Hancock County, Ohio							3,985 (C)	1,994 (C)	(C)	(C)
Lenawee County, Mich							3,985 (C)	1,986 (C)	(C)	(C)
Henry County, Ohio								4,974 (C)	959 (C)	(C)

[1] All releases were made prior to June 15.
[2] (R) indicates that adults were recovered in the spring following the releases.
[3] (C) indicates that collections were made in the spring following the date specified but no adults were recovered.

It will be seen that adults were recovered in only 2 localities out of the 12, and that in both these localities recoveries were made in 2 successive years, each in the spring following fall releases of the parasite, in other words without the intervention of an entire season between release of adult parasites and subsequent rearing from field-collected borers. The only instance of a fall release in which no adults were recovered was at Lucas County, Ohio, in 1928. In this case, however, the entire supply of cornstalks in the field was not placed in cages, as was done in the localities where recoveries were made.

These observations, while substantiating the conclusion reached as a result of the biological studies, that the parasite can successfully overwinter in the Lake Erie environment, strongly indicate that permanent establishment was not attained. No recoveries were ever obtained at any of the points listed in table 11, unless, as indicated above, releases were made after the completion of the critical summer developmental period. In many of these centers of liberation there was without doubt satisfactory initial parasitization of the borers available at the time of the release. Such parasitization as did occur, however, would not be permanent because of nonharmony of developmental phases of *E. roborator* and *P. nubilalis* from June 15 to August 10, or probably later, since August 10 is the earliest date in the area under observation when host development has progressed to a point that will permit the parasite to exist.

Data on further releases of *Exeristes roborator* adults in this area are presented in table 12. Although recovery attempts at these points do not approach in adequacy those previously discussed, a similar lack of permanent establishment of the species is evident. A few recoveries were made immediately after the release of adults, but succeeding attempts were unsuccessful.

TABLE 12.—*Releases of Exeristes roborator at all points at which only limited recovery attempts have been made*

Locality	Parasites liberated	Locality	Parasites liberated
	Number		*Number*
Lake County, Ohio	[1] 15,208 (5)	Wayne County, Mich	1,847 (1)
Erie County, N.Y	11,519 (5)	Macomb County, Mich	1,910 (1)
Erie County, Pa	8,433 (3)	Jackson County, Mich	1,682 (1)
De Kalb County, Ind	13,002 (5)	Elkhart County, Ind	3,823 (2)
Lorain County, Ohio	1,009 (1)	Will County, Ill	2,302 (2)
Washtenaw County, Mich	11,730 (3)	Ottawa County, Ohio	1,726 (1)
Huron County, Ohio	11,832 (3)	Wood County, Ohio	1,745 (1)
Genesee County, N.Y	10,977 (3)	Ashtabula County, Ohio	1,919 (1)
Crawford County, Pa	11,686 (3)	Jefferson County, N.Y	1,955 (1)

[1] Figures in parenthesis indicate the number of years in which releases were made.

SUMMARY

Exeristes roborator, an external ichneumonid parasite of the European corn borer, is generally distributed throughout Europe and has been imported and extensively liberated in the United States.

A laboratory environment of 80° F. and 70 percent relative humidity is near the optimum for the parasite's development. Variations

from this environment in either temperature or moisture tend to react adversely, particularly if the variation is toward higher temperatures not accompanied by higher relative humidities.

Many factors contribute to the occurrence of a diapause in the larval stage of this parasite, but apparently no single factor entirely controls it. The parasite best survives the diapause when it is kept in an environment conducive to slow development as produced by temperatures of 33° to 36° F.

The adult female first paralyzes the host larva and then deposits an egg on or in close proximity to it. Little preference is shown in the selection of a host, but only fifth-instar larvae will support the parasite to maturity. Hatching and all larval development occur externally upon the host.

Exeristes roborator can be reared in the laboratory in sufficient numbers to permit extensive liberations in the field for the purpose of determining its importance in corn-borer control. The method consists of transferring the parasite eggs from the oviposition medium onto host larvae that have been paralyzed by immersion for 10 minutes in hot water at exactly 49° C. (120.2° F.). During hatching and development an environment of 80° F. and 70 percent relative humidity is maintained. To permit extended breeding periods followed by emergence of adults over the comparatively short liberation period, developing material may be stored in an environment having a temperature range from 32° to 40° F. and a relative-humidity range from 75 to 90 percent. Pupae and larvae that undergo a diapause, particularly the latter, react to this treatment better than do other forms.

It appears from field studies, for the most part conducted under controlled field-plat conditions, that the factors limiting the effectiveness of the parasite in controlling the European corn borer in the Lake Erie area are the nonharmony of the seasonal cycle of the parasite and that of its host, *Pyrausta nubilalis*, the nonharmony of the seasonal cycle of the parasite and that of other known potential hosts, and the low biotic potential of the parasite under field conditions.

Although *Exeristes roborator* has been extensively liberated throughout the territory infested by the corn borer in the United States, and has become initially established in many instances, there is no evidence that the parasite can maintain itself in any environment within the limits of the present (1933) infested areas or that it is likely to be of more than insignificant importance among the general influences affecting the abundance of *Pyrausta nubilalis*.

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